TYPES OF BLIND VEIN-ENDINGS IN THE DICHOTOMOUS VENATION OF CIRCAEASTER

ADRIANCE S. FOSTER

A SALIENT FEATURE of the predominantly reticulate venation patterns of many dicotyledons as well as certain monocotyledons is the presence of blind vein-endings within the numerous areoles of the vascular system. Pray (1963) has treated in great detail the morphology and histogenesis of such vascular terminations in the leaves of *Liriodendron*, *Aucuba*, and *Smilax*. He concluded that "it seems probable that development of the minor venation of all angiosperms which have reticulate patterns similar to those investigated here involves similar ontogenetic processes."

In the highly contrasted dichotomous venation patterns of *Kingdonia* and *Circaeaster*, however, the majority of the ultimate veinlets terminate in marginal teeth, vein anastomoses are infrequent and when areoles are formed, they are devoid of included vein-endings (Foster 1959, 1963, 1966, 1968; Foster & Arnott 1960). In describing this type of venation, I used the expression "blind vein-endings" to designate those veinlets which terminate in various positions and levels without reference to any of the distal marginal teeth. Do such blind vein-endings represent the vascular supply of "arrested" marginal teeth, or should they be considered as "supplementary veins" which are characteristic of "open" dichotomous venation in general?

The present article describes and seeks to interpret morphologically the various types of blind vein-endings encountered in my extensive surveys of cultivated plants of *Circaeaster agrestis* Maxim. My original investigation of herbarium material revealed very few examples of blind vein-endings, although it was admitted that their apparent rarity might have been the result of insufficient leaf sampling (Foster 1963, pp. 310, 311). In the leaves obtained from successive populations of *Circaeaster* raised in the growth chamber and in the Botanical Garden of the University of California during the past four years, however, blind vein-endings were relatively frequent. Not only were unbranched marginal and central endings found, comparable to some of those previously described, but a totally unexpected type of marginal, blind, dichotomously branched ending was discovered. This novel aspect of the venation of *Circaeaster* has been very carefully studied and constitutes a point of particular emphasis in the present paper.

MATERIALS AND METHODS

Ripe fruits, collected from the 1967 population of cultivated plants, were sown in large pots and 128 plants were raised from seedlings to maturity, in a growth chamber in which a photoperiod of 16 hours and a constant temperature of 50° F. were maintained. This temperature, which was about 10° higher than that employed in previous years, appeared to be a very significant factor in the unusually vigorous growth of the 1968 plants.

At maturity, the plants were harvested and the leaf-rosettes preserved in 70% alcohol. A total of 6,179 leaves (including the larger floral bracts) were dissected from these specimens, examined for anastomoses and blind vein-endings, and the data recorded in tabular form. Leaves which were selected as the basis for the illustrations in this paper were cleared in NaOH followed by concentrated chloral hydrate, thoroughly dehydrated in the alcohol-series, and stained in a 1% solution of safranin in equal parts of absolute alcohol-xylene. Some of the leaves however were very difficult to clear satisfactorily in low concentrations of NaOH (i.e., 2.5%–5%) because of peculiar "amorphous" inclusions in many of the parenchyma and epidermal cells. Prolonged treatment in cold 10% NaOH (for 3 weeks or longer) followed by chloral hydrate in most instances improved the appearance of such leaves prior to staining. In order to secure evenly stained preparations for subsequent photography, the leaf-specimens were left in the safranin for a relatively short period, approximately 1½ to 2 hours rather than overnight as in the case of most of the leaves processed in previous years. This shorter period in the stain gave excellent preparations, especially when the destaining was done in a mixture of 3 parts of xylene to 1 part of absolute alcohol. This solution prevented the too rapid leaching of safranin which always tends to occur when a mixture of equal parts of xylene-alcohol is used for destaining.

I am grateful to Mrs. Irene Baker for her invaluable assistance in dealing with the germination and culture of the plants in the growth chamber. Thanks are also due Mr. Alfred A. Blaker, who made the photomicrographs, and Mrs. Emily E. Reid for preparing and arranging the line drawings. I am also very appreciative of my wife's assistance in proof-reading the manuscript.

Symmetrical Patterns of Dichotomous Venation

Comprehensive surveys of leaf morphology in herbarium collections and cultivated plants of *Circaeaster* have clearly shown the considerable fluctuation in (a) the shape of the lamina, (b) the number of teeth at the distal margin, and (c) the degree of symmetry of the venation patterns (Foster 1963, 1966, 1968). In many of the leaves obtained from herbarium material, the lamina is flabelliform or broadly ovate in contrast to the frequently narrower obovate or spatulate contour of the leaf-blade developed in the various populations of cultivated plants. Despite the variation in form and symmetry of the lamina, however, it is evident that usually all the vein-endings in a given leaf terminate in corresponding marginal teeth. This type of one-to-one correlation tends to predominate regardless of whether an even or an odd number of marginal teeth is present. It is,

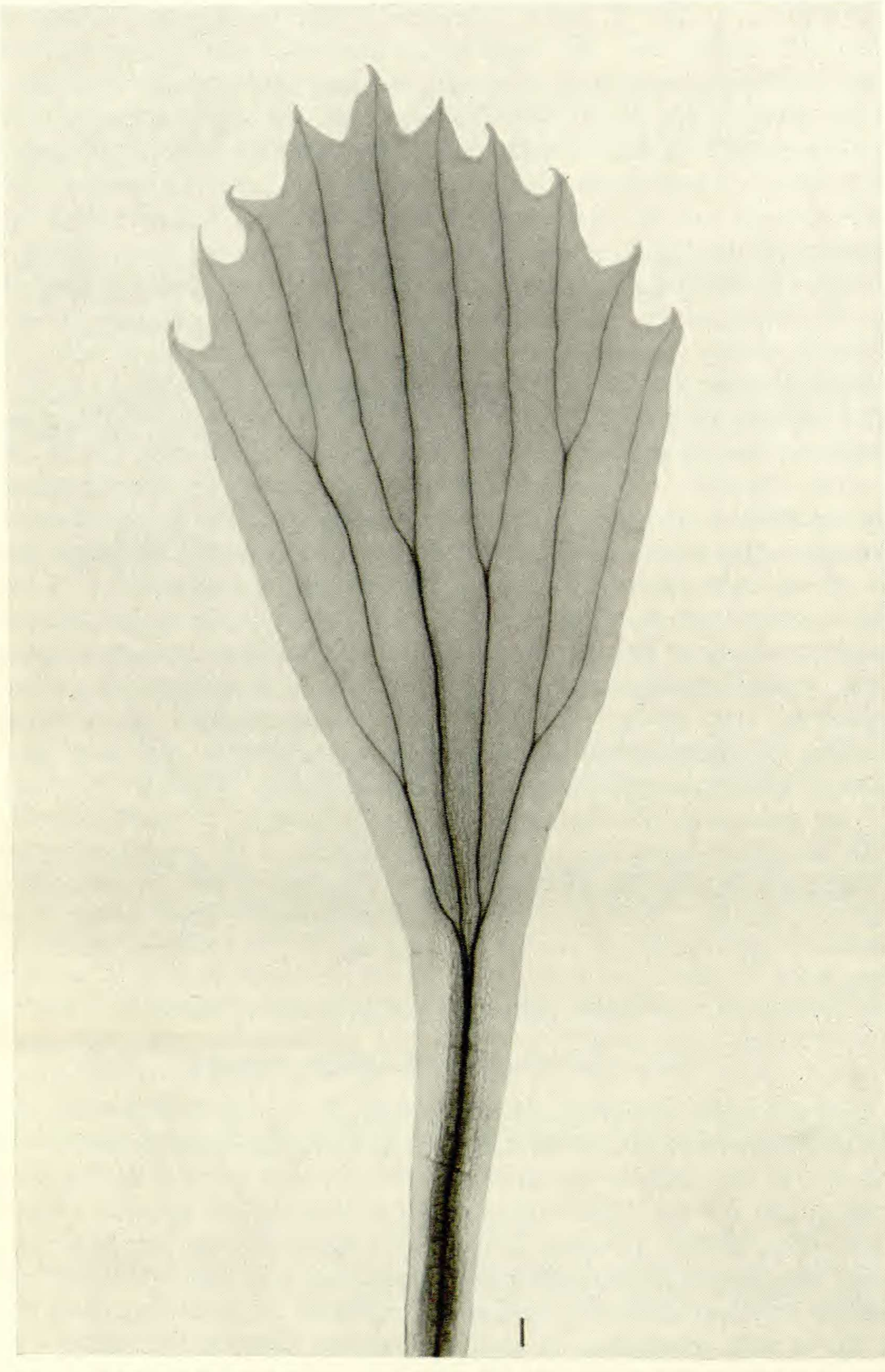

FIG. 1. Cleared leaf with symmetrical open dichotomous venation. Bifurcation of the petiolar bundle at base of lamina yields two "identical" types of vein-systems, each composed of five veinlets terminating in corresponding marginal teeth, × 8.6.

however, particularly striking in those cases where the associated pattern of dichotomous venation is symmetrical (Foster 1963, *Pl. I, fig. 5*).

An unusually clear example of "isotomous" venation is shown in FIGURE 1. In this leaf, the bifurcation of the petiolar bundle is followed by the dichotomy of each branch, resulting in two symmetrical pairs of veins at the base of the lamina. From each pair of basal veins, by appropriate dichotomy at successive and approximately opposite levels, two "identical" systems of veins are produced. Each system consists of a long unbranched marginal strand and two pairs of additional veins *all* of which enter corresponding marginal teeth. The two halves or "sectors" of the lamina are thus vascularized by corresponding vein-systems which are separated from each other by a long, well defined "neutral space." This term was used by Bock (1962, pp. 9 and 10, *Figs. 15, 17*) to designate the non-vascularized area between two vein-systems in leaves with symmetrical dichotomous venation. In this connection, the basic morphological resemblance between the venation pattern shown in FIGURE 1 and that of the leaf of *Ginkgo* and a pinnule of *Adiantum* is indeed remarkable (see Bock 1962, *Fig. 13a, b*).

Unbranched Blind Vein-endings

Blind vein-endings in the leaves of *Circaeaster* may be conveniently classified into two main "types" viz.: branched and unbranched. The first type, to be described later, is relatively infrequent and has only been observed in a few leaves of cultivated plants (FIGS. 16–22, 29). In contrast, unbranched blind endings are rather commonly seen and occur in a great many leaves of the plants which were raised in the growth chamber during 1968 (FIG. 2).

It must be emphasized in the first place that the presence or absence of blind vein-endings is obviously not correlated with the size or shape of a leaf or its relative position in the leaf-rosette. Comparatively small primary leaves with only a few teeth may develop one or more blind endings (FIG. 3) and similar endings may occur in floral bracts (FIG. 4) and larger foliage leaves (FIGS. 5–8).

With reference to their general position in the venation pattern, unbranched vein-endings apparently occur most commonly in the lateral marginal region of the lamina. In some cases there is only a single blind ending in a leaf (FIGS. 4, 6, 7, 8, 10) but a number of examples have been found where a blind ending is present in each margin of the lamina (FIGS. 3, 5, 11). Considerable variation exists with respect to the level of divergence and the relative length of unbranched marginal blind endings. Often the ending is very short and diverges at a relatively high level in the lamina (FIG. 2, at right). But a good many examples have been found of marginal endings which diverge at the very base of the lamina. In these cases the marginal veins may terminate blindly after extending only a short distance along the margin (FIGS. 3, 5). In other leaves, however, the blind ending may be more highly developed and extend nearly the full length of the lateral margin (FIGS. 10, 11). Marginal blind endings, more or less intermediate in length between these extremes also occur and are shown at the left of FIGURES 7 and 8.

Less frequently, unbranched blind vein-endings occur in the upper central region or even in the distal margin of the lamina. In certain leaves which were studied, blind vein-endings are restricted to the central portion of the lamina (FIG. 13), while in others, both marginal and central blind endings occur in the same lamina (FIGS. 2, 12, 14). One of the most remarkable examples I have seen of a distal blind vein-ending is represented in FIGURE 15. In this leaf, the short acroscopic branch of a very symmetrical vein-dichotomy ends blindly, as shown by the arrow, *between* two adjacent teeth. It is also evident that central blind endings, as represented in FIGURES 2, 13, 14, commonly terminate at varying distances *below* the narrow sinuses between adjacent marginal teeth.

During the course of this investigation a very careful search was made to discover whether the development of unbranched blind vein-endings was ever correlated with the presence of corresponding vestigial marginal teeth. *A priori* it might be anticipated that since the sister-branch of a marginal or central blind ending enters a corresponding tooth, or by further dichotomous branching vascularizes several successive teeth, the blind ending itself might represent the vascular supply of an undeveloped or rudimentary tooth. But only a single possible correlation of this sort was encountered (FIGS. 6, 9). However, the peculiar massive cluster of tracheary elements found at the base of this vestigial tooth raises certain problems which will be more appropriately considered later in the discussion section of this paper.

Marginal Blind Dichotoms

As mentioned in the introduction of this paper, one of the most unexpected results of my venation survey was the discovery of a dichotomously branched type of blind vein-ending in the lateral margin of the lamina of certain leaves (FIGS. 16–22). In order to relate such ramified endings to the overall pattern of dichotomous venation in *Circaeaster*, I have adopted Bock's (1962) term "dichotom." This term, which is brief and convenient for descriptive purposes is defined by Bock (1962, p. 6, *Fig. 1*) as follows: "As a general principle, *dichotomy* should be considered a growth pattern in which a base member develops two branch members, both advancing in a direction different from that of the base member. . . . The two angles formed by the base and the two branches may be equal, but also may vary. They are called the base angles, being always paired, while the angle formed by the two branches is the branch angle. Such a single dichotomy is called a *dichotom*."

In applying Bock's general concept to the venation patterns shown in FIGURES 16 to 22, the following interesting morphological differences between the various forms of marginal blind dichotoms are quite evident, viz:

1. POINT OF ORIGIN OF THE BLIND DICHOTOM. In the leaves depicted in FIGURES 19 and 22, the "base member" of the dichotom is a relatively long

major lateral vein which bifurcates in the lower marginal region of the lamina. In contrast, the "base member" of the blind dichotom in the other five leaves represents the *outer branch of a lateral vein-dichotomy* which originates near the lamina base. In each of these cases, the sister-branch of the blind dichotom, by means of further dichotomous branching, forms two or three vein-endings which vascularize corresponding lamina teeth (FIGS. 16, 17, 18, 20, 21).

2. LENGTH AND SYMMETRY OF DICHOTOM-BRANCHES. In one of the leaves, the two "branch members" of the dichotom are extremely symmetrical and approximately equal in length (FIGS. 18, 25). But in all the other examples, the *inner* (i.e. submarginal) "branch member" is more or less conspicuously longer than its sister-branch. This remarkable asymmetry is obvious in dichotoms with relatively short branches (FIGS. 16, 19, 20, 24, 26) but is particularly striking when the inner branch terminates near the dentate margin of the lamina (FIGS. 17, 21, 22, 23).

3. MODE OF TERMINATION OF DICHOTOM-BRANCHES. As in the case of unbranched vein-endings, close attention was given to the possible association of blind dichotoms with corresponding rudimentary marginal teeth. Careful study of the venation under high magnification showed that in six of the leaves, the terminal tracheary elements of the dichotom-branches end freely in the mesophyll and that no histological evidence exists of vestigial teeth above such endings (FIGS. 23, 24, 26). In one leaf, however, as shown in detail in FIGURE 25, a peculiar "shelf-like" projection of the lamina margin lies directly above the outer branch of the blind dichotom. Whether this "shelf" should be regarded as a "rudimentary tooth" is extremely problematical. When the projection was carefully examined under higher magnification than is represented in FIGURE 25, it was found completely devoid of tracheary elements and in this respect quite unlike the apparently "authentic" vestigial tooth shown in FIGURE 9.

DISCUSSION

The varied types of blind vein-endings which have just been described, collectively represent a puzzling aspect of the dichotomous venation pattern of *Circaeaster*. Since usually all the vein-endings in a given leaf enter corresponding marginal teeth, the blind endings which may additionally occur in various regions of the lamina pose interesting morphological and ontogenetic questions.

From the standpoint of a morphological analysis of the *mature venation*, an unbranched blind ending in most instances appears to represent the shorter and usually less well-developed branch of a typical vein-dichotomy. In the simplest case the "dichotom" which yields a blind ending is very symmetrical in organization, one of its branches entering a marginal tooth, the other terminating at various levels in the lateral margin of the lamina (FIGS. 2, 11, at right). More complex patterns result when the sister-branch of the blind ending forks once or twice, forming terminal veinlets which enter two or three adjacent teeth (e.g. FIGS. 4, 7, 8, 10). Comparable variations in venation pattern and in the degree of development of the blind ending also occur in the central or distal portions of the lamina (FIGS. 2, 12–15).

It is tempting, in the case of unbranched blind vein-endings, to speculate that they may represent the *persistence* of the vascular supply of "suppressed" marginal teeth. The present investigation, however, gives little real support to such an assumption.

In the first place, the majority of the marginal blind endings are more or less strictly parallel with the edge of the lamina and terminate without reference to any protuberance which would qualify as the "rudiment" of a tooth (FIGS. 2, 4, 5, 7, 8, 10, 11). Only one leaf was encountered in my entire survey in which a diminutive tooth is situated *above* the tip of a long marginal blind ending. (FIG. 6). However, since the longitudinal course of differentiation of xylem in the veins entering "normal" leaf teeth has not been determined, the significance of the *isolated* cluster of tracheary elements at the base of this vestigial tooth remains obscure (FIG. 9). Such an irregular and exaggerated development of the primary xylem does not occur, for example, at the point of entrance of a vein into a well developed tooth, nor is it matched in those puzzling cases where a tooth is vascularized by a basally unconnected strand (FIG. 19, right margin).

Secondly, some of the vein-endings terminate very near the branch of a vein-dichotomy, suggesting that they may represent the incomplete development of Type V anastomoses rather than the vascular supply of "arrested" teeth (FIG. 11, at left margin; FIG. 12, upper center). A further example of this interesting condition has already been described in a recent paper on anastomoses in *Circaeaster* (Foster 1968, p. 61 and *Fig. 15*).

Most of the objections which have just been raised against interpreting unbranched blind endings as the vascular supply of "arrested" teeth are also valid with respect to the morphological nature of marginal blind dichotoms (FIGS. 16–22, 29). In the comparatively few leaves which had formed such ramified endings, there was no evidence of paired vestigial teeth and only one instance, as shown in FIGURE 25, of a peculiar shelf-like extension of the margin above the dichotom. This "shelf," however, lacks vasculature and does not seem to qualify as a rudimentary tooth; its morphological "significance," if any, is highly problematical.

From a comparative viewpoint it is important to note the occurrence of blind vein-endings in the dichotomous venation of other plants. *Kingdonia* is a good example for comparison because of the abundance and consistent development of blind endings in the dichotomously veined segments of its relatively large lamina (Foster 1959, Foster & Arnott 1960). Although the majority of the terminal veinlets enter corresponding marginal teeth, as in the smaller lamina of *Circaeaster*, 14.2% of all vein-endings studied in *Kingdonia* terminated blindly at various levels and positions in the lamina segments. Very commonly, the blind ending reaches the side or base of the sinus which separates adjacent marginal teeth (Foster & Arnott 1960, *Fig. 14*). But one of the most interesting points of similarity between *Circaeaster* and *Kingdonia* is the occurrence in both genera of marginal blind dichotoms. FIGURE 27 represents the enlargement of a small part of the margin of a lamina segment of *Kingdonia.* The branches of the conspicuous blind dichotom shown in this figure are unequal and, as in *Circaeaster*, the inner branch is much longer than the outer (compare FIG. 27 with FIGS. 22 and 23). It is also notable that each of the lateral veins of the small tepals of the flower of *Kingdonia* may dichotomize and form two unequal freely terminating branches very much like the branching pattern of some of the marginal dichotoms of *Circaeaster* (Foster 1961, p. 402, *Figs. 4a, 5*).

When one seeks for additional examples of blind vein-endings in dichotomous venation patterns, the genus *Adiantum* comes to mind as worthy of study. In *A. capillus-veneris* L. the great majority of the vein-endings extend into corresponding marginal teeth, as in *Circaeaster*, and blind-endings are apparently rare in occurrence (Knobloch & Correll 1962, *Plate 13, Fig. 1*). My own extremely limited investigations on *A. cooperi* Baker, a species native to Costa Rica, revealed striking examples of marginal blind dichotoms, very similar to those in the leaves of *Circaeaster* and *Kingdonia* (FIG. 28). This is clearly a remarkable example of parallel evolution, comparable to the similarity between the types of vein-anastomoses in *Circaeaster* and those in such unrelated taxa as *Anemia*, *Zamia* and *Ginkgo* (Foster 1968, pp. 63–65). In this connection, it is of interest to note that Arnott (1959, p. 408 and *Fig. 9*), in his intensive study of dichotomous venation in *Ginkgo*, found examples of "veins ending a considerable distance from the margin." Such veins seem entirely comparable to the central blind endings which may develop in *Circaeaster* (compare Arnott's *Fig. 9* with FIGS. 2 and 13 of the present paper).

In conclusion, the need for thorough ontogenetic studies on the time of origin and mode of differentiation of blind vein-endings in dichotomous vasculature should be strongly emphasized. It would certainly be of morphological interest, in the case of *Circaeaster*, for example, to know (1) how strictly the initiation and development of marginal teeth is *coordinated* with the *pattern of differentiation* of dichotomous venation and (2) the time of origin and the longitudinal course of development of the various types of blind vein-endings. Whether detailed information on these problems would also shed light on the phylogenetic significance of dichotomous venation in *Circaeaster* remains, however, in my opinion, a completely open question.

[*Postscript to original manuscript*]

After the manuscript of the present paper had been completed, a remarkable type of marginal blind dichotom was found in which the *outer*, rather than the inner branch, was conspicuously longer than its sister branch (FIGURE 29). Whether this type of asymmetrical vein dichotomy is "exceptional" or is as frequent in occurrence as the marginal dichotoms illustrated in FIGURES 16–26 of this paper, remains to be determined by further surveys of leaf venation in *Circaeaster*.

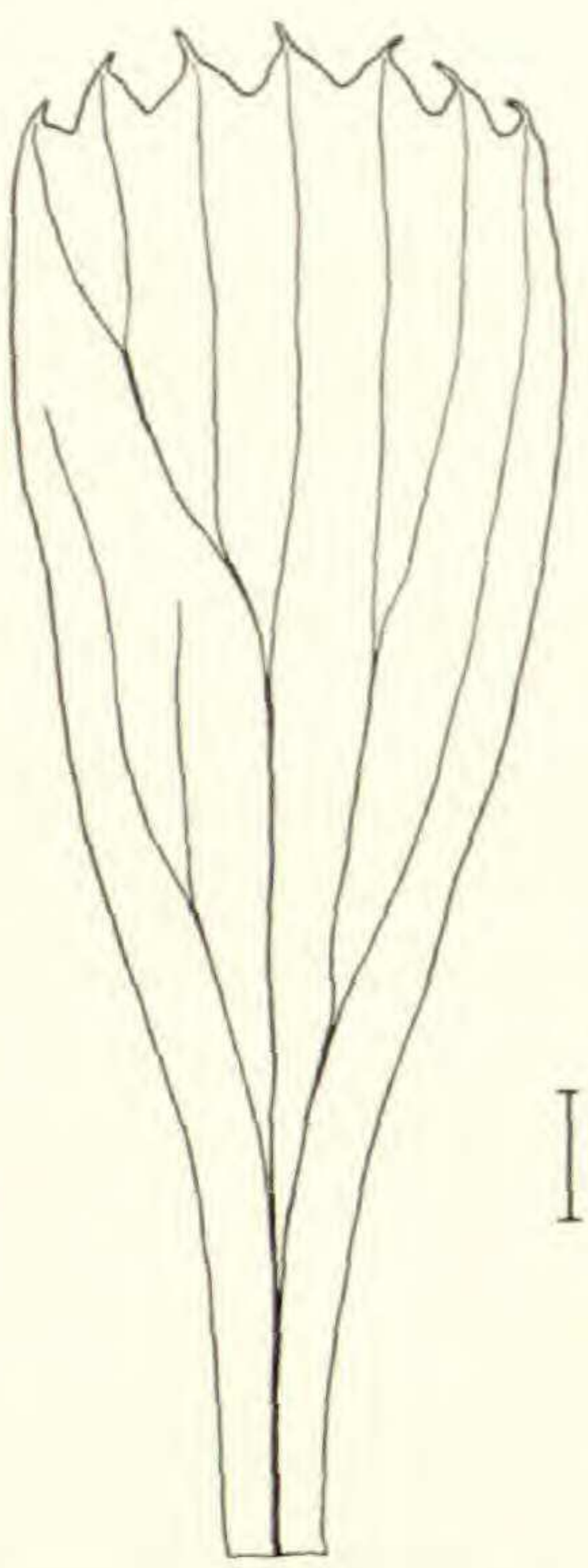

FIGURE 29. Leaf with conspicuous asymmetrical blind dichotom which represents the bifurcation of the basal vein at the *left* of the lamina. Note that the basal vein at the *right* has formed three veinlets which terminate in corresponding teeth at the distal margin of the lamina. The scale at the side of the drawing equals 1 mm.

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DEPARTMENT OF BOTANY
UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA 94720

EXPLANATION OF PLATES

PLATE I

Fig. 2. Leaf with two blind vein-endings, one in upper central region of lamina, the other in the margin at right. Note that the petiolar bundle dichotomizes far below the lamina-base, forming two asymmetrical vein-systems, × 15.8.

PLATE II

Figs. 3–8. Leaves with marginal blind vein-endings. Fig. 3. Primary leaf with a blind vein-ending at each margin. Fig. 4. Floral bract with relatively long blind ending at right margin. Fig. 5. Leaf with eight symmetrically-vascularized teeth and a blind vein-ending at each margin. Note particularly the very low level of divergence of the blind ending at right. Fig. 6. Leaf with long blind vein-ending and very rudimentary tooth (indicated by arrow) at left margin. The structural details of the cluster of tracheary elements found at base of this tooth are shown in Fig. 9. Fig. 7. Leaf with eight symmetrically-aligned teeth and an unbranched vein-ending at left margin. Fig. 8. Leaf with two well-defined vein systems, the one at left with a long marginal blind ending. Note also vein-approximation at lower left of lamina. The scale at the side of each drawing equals 1 mm.

PLATE III

Fig. 9. Highly magnified view of the cluster of tracheary elements at the base of the vestigial lateral tooth of the leaf shown in Fig. 6, × 250.

PLATE IV

Figs. 10–15. Leaves illustrating diversity in position and number of blind endings. Fig. 10. Leaf with ten symmetrically vascularized teeth and a long blind ending at left margin. Fig. 11. Leaf with eight symmetrically aligned teeth and two marginal blind vein-endings. Fig. 12. A leaf with two blind endings, one in central region of lamina, the other at the right margin. Fig. 13. Leaf with two unequal blind vein-endings, both in upper central portion of lamina. Fig. 14. Asymmetrical lamina with three blind endings, one at left margin, the other two in upper central area. Fig. 15. Leaf with asymmetrical lamina showing two blind vein-endings, one very short and rudimentary in upper central region, the other, indicated by arrow, terminating *between* two teeth at left. Note conspicuous Type I anastomosis in this leaf and short unconnected xylem strand (represented as a short isolated black line near distal margin of lamina). The scale at the side of each drawing equals 1 mm.

PLATE V

Figs. 16–22. Leaves illustrating marginal blind dichotoms. Fig. 16. Dichotom, at left margin, with nearly equal branches. Details shown in Fig. 24. Fig. 17. Dichotom, at right margin, with unequal branches, the longer terminating below vascularized tooth. See Fig. 23 for details. Fig. 18. Leaf with very symmetrical blind dichotom at left margin. See Fig. 25 for details. Fig. 19. Dichotom, at left margin, with unequal branches represented in more detail in Fig. 26. Note that outermost tooth at right is vascularized by an unconnected strand (*US*). Fig. 20. Leaf with an unusual combination of an unbranched blind-ending at right margin and a symmetrical blind dichotom at left margin of lamina. Fig. 21. Dichotom, with unequal branches, at left margin of lamina. Fig. 22. Dichotom, at right margin of lamina, with conspicuously unequal branches. This leaf and the one shown in Fig. 7 are from the same plant. The scale at the side of each drawing equals 1 mm.

PLATE VI

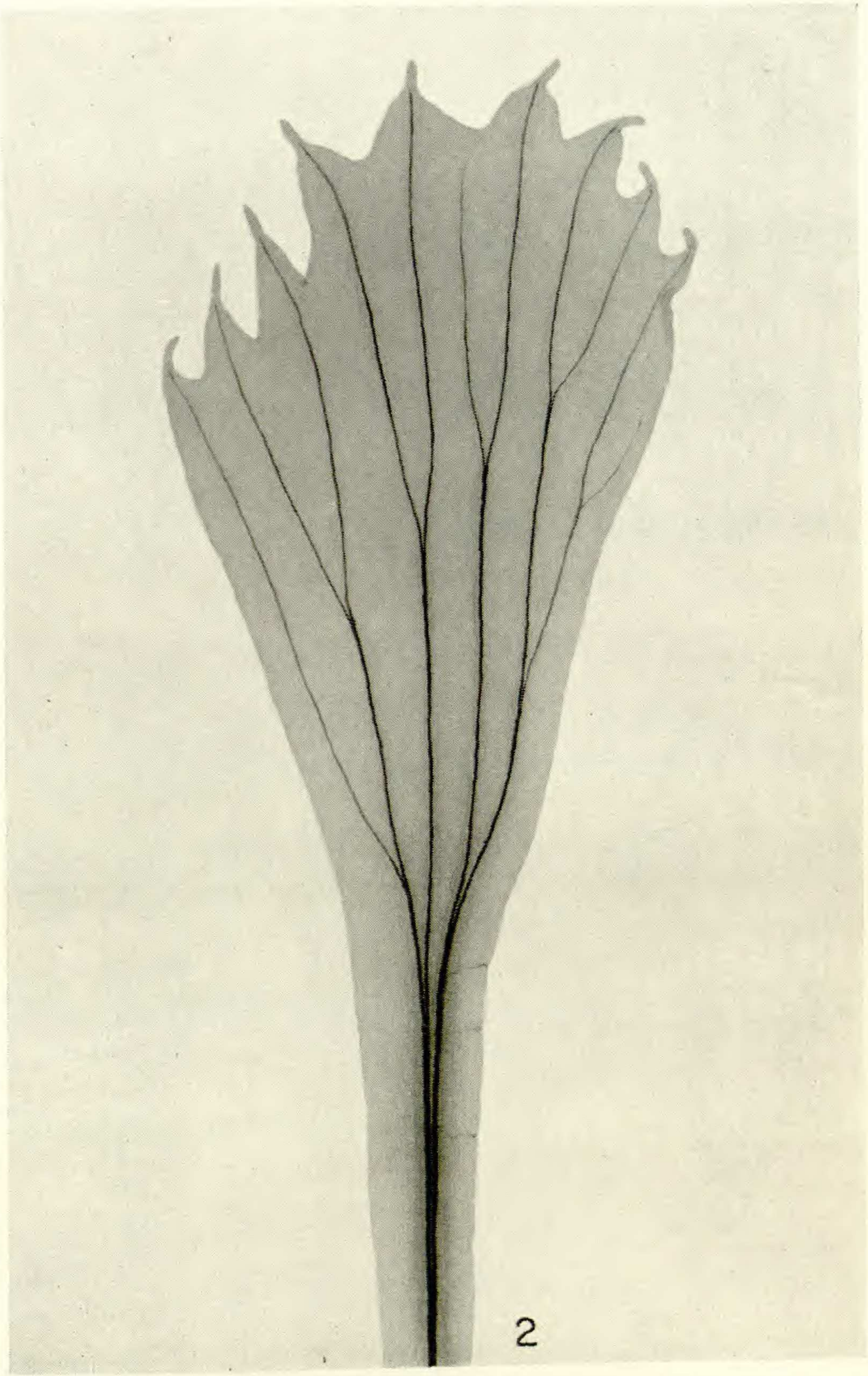
Marginal blind dichotoms. FIG. 23. Structural details of dichotom of leaf shown in FIG. 17, × 49. FIG. 24. Magnified view of dichotom of leaf represented in Fig. 16, × 40.

PLATE VII

Marginal blind dichotoms. FIG. 25. Structural details of the very symmetrical marginal dichotom of the leaf shown in FIG. 18. Note that the dichotom terminates a short distance below a shelf-like projection of the lamina-margin, × 54. FIG. 26. Greatly enlarged view of dichotom of leaf represented in FIG. 19, × 67.

PLATE VIII

FIG. 27. Portion of marginal region of lamina segment of *Kingdonia uniflora* showing blind dichotom similar in type to that in leaf of *Circaeaster*, represented in FIG. 23, × 15.5. FIG. 28. Marginal region of pinnule of *Adiantum cooperi*, showing at lower left, a blind dichotom. Note remarkable similarity to blind dichotoms of *Circaeaster* shown in FIGS. 17, 19, and 22, × 15.5.



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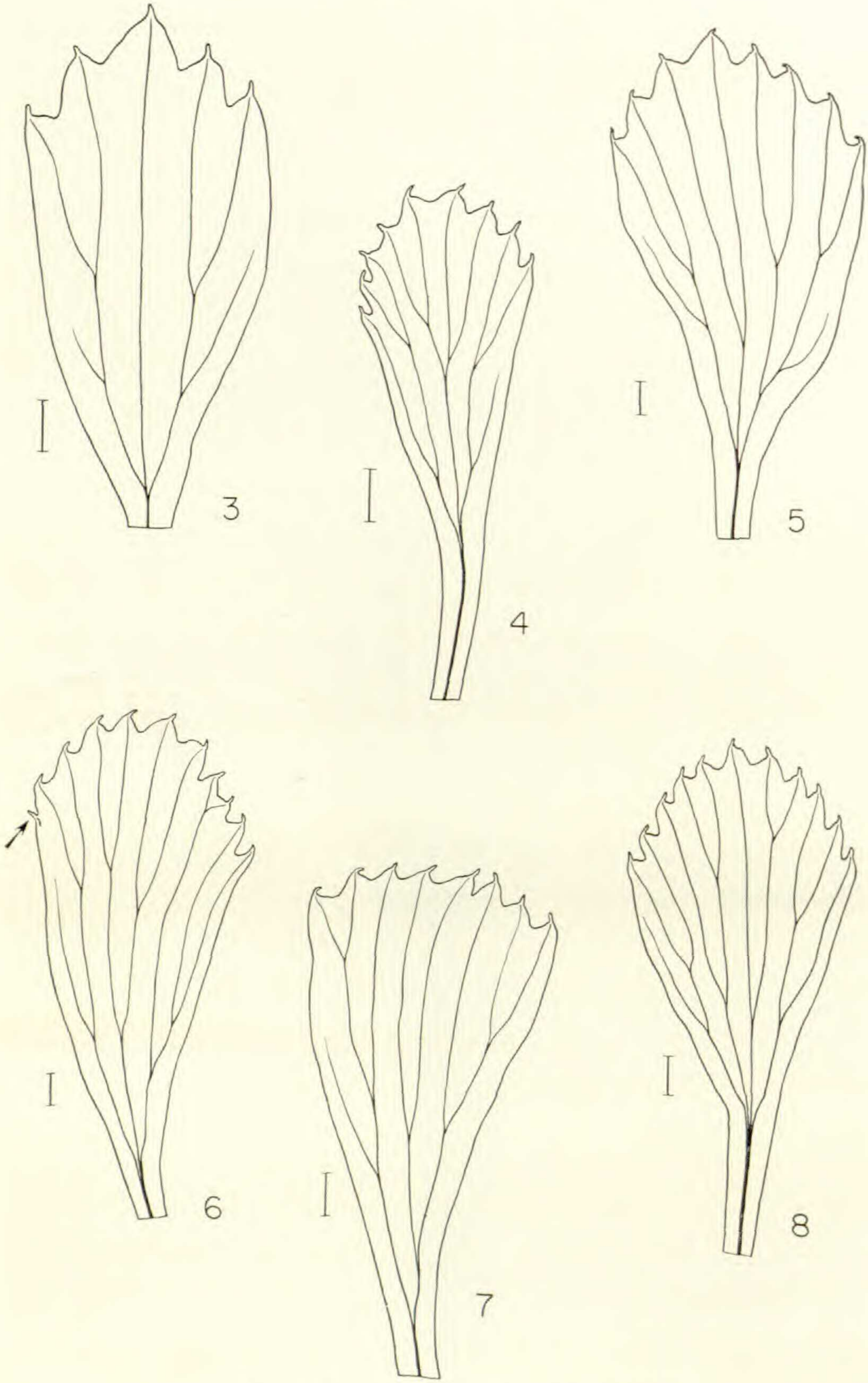

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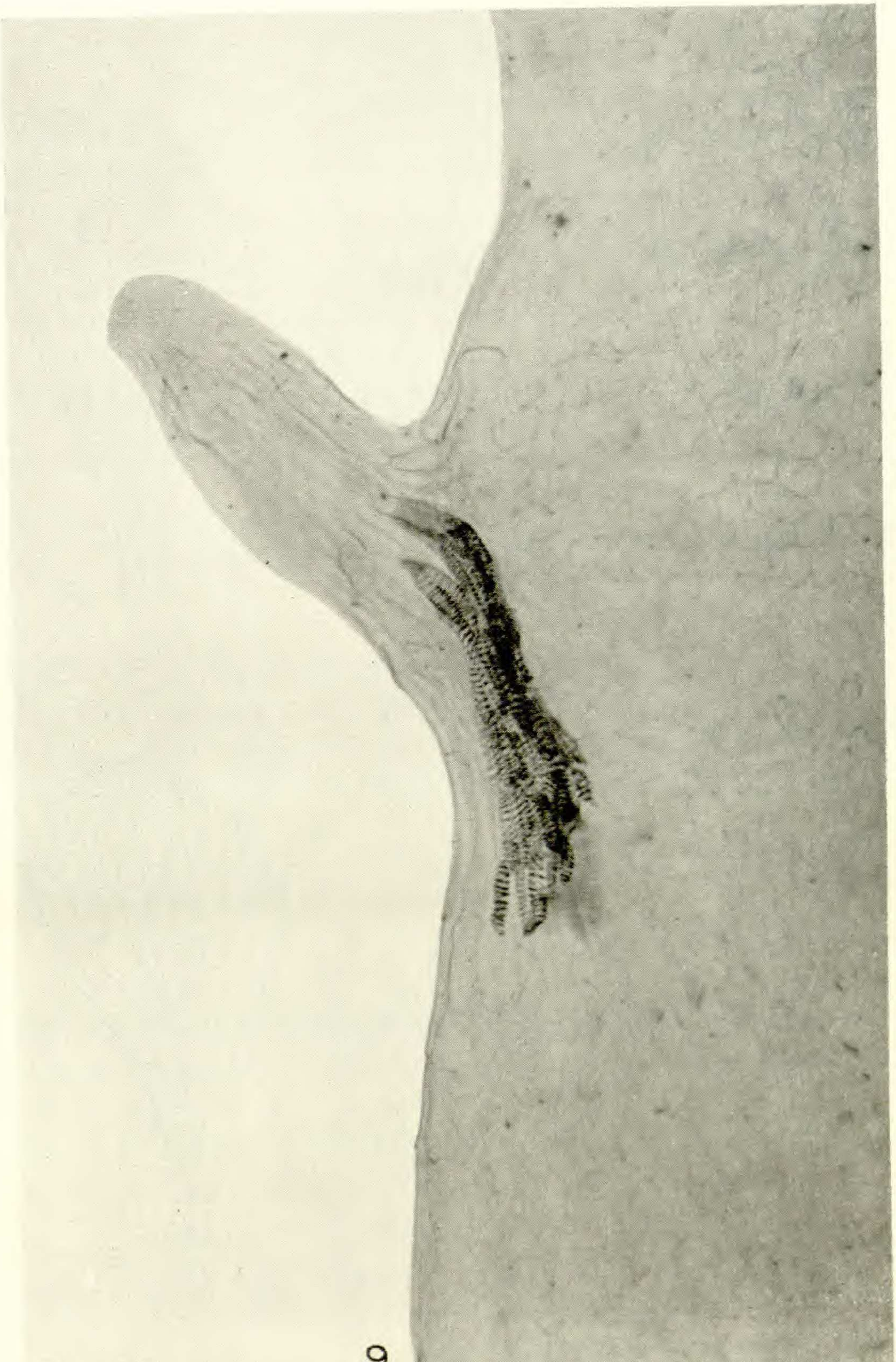

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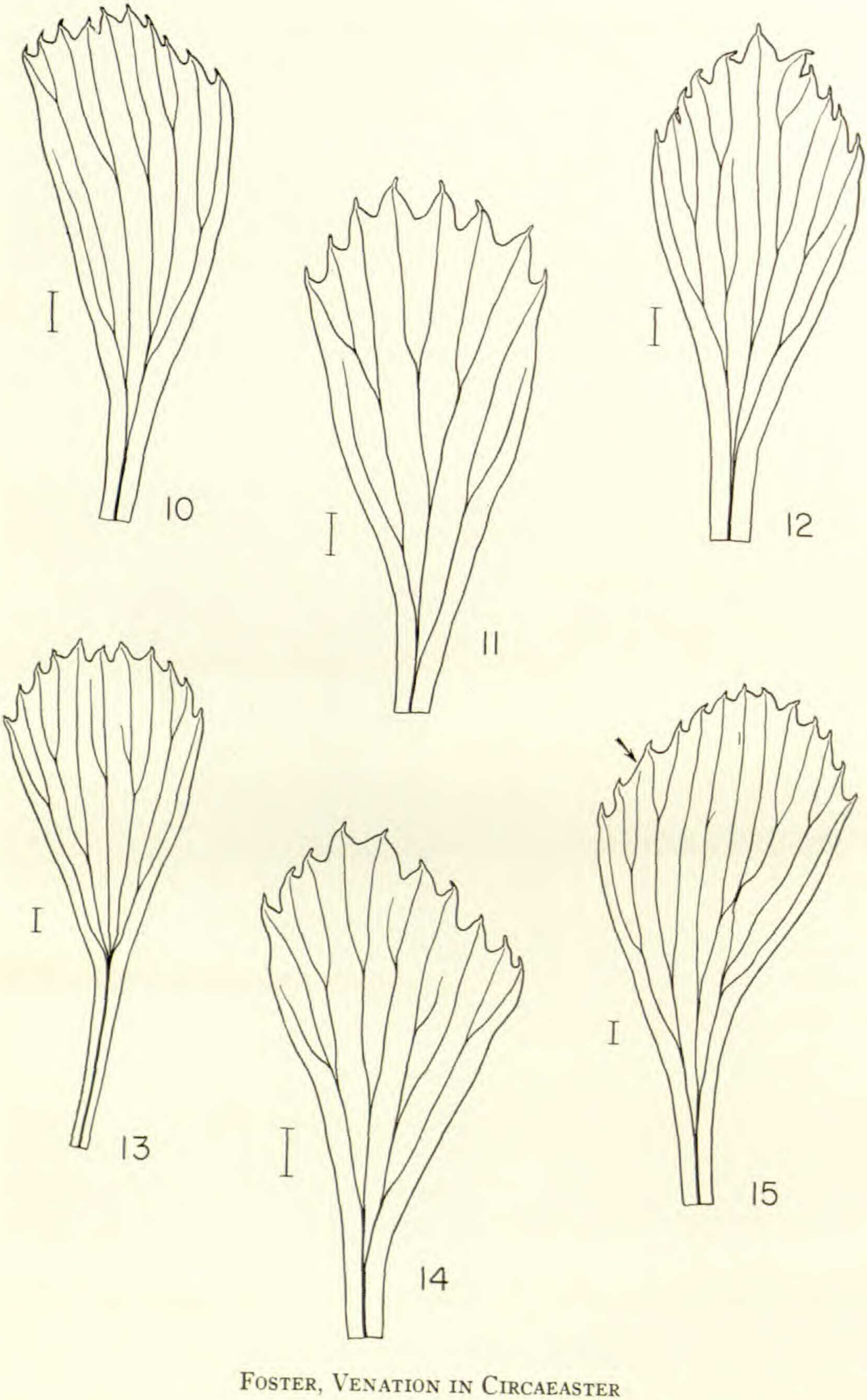

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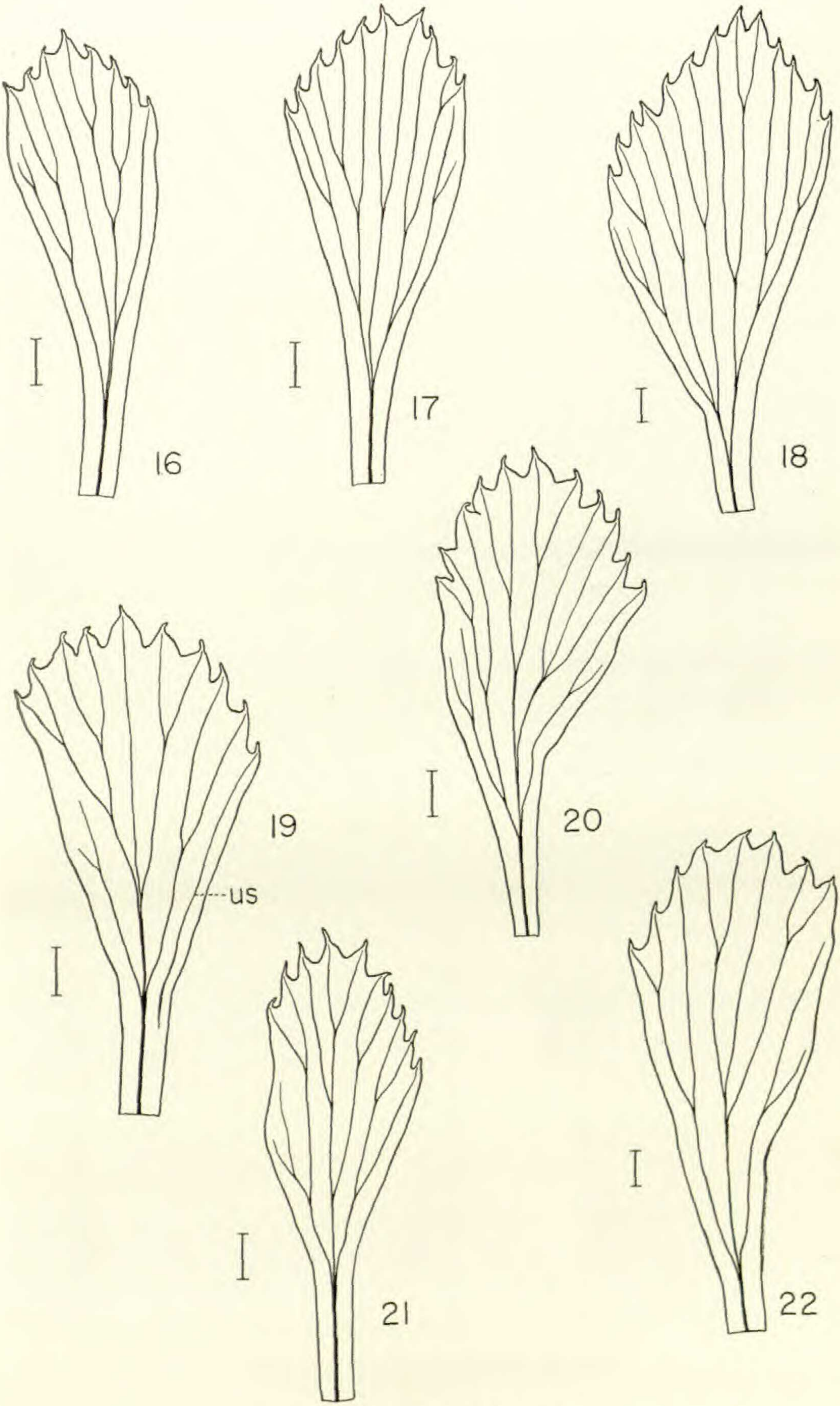

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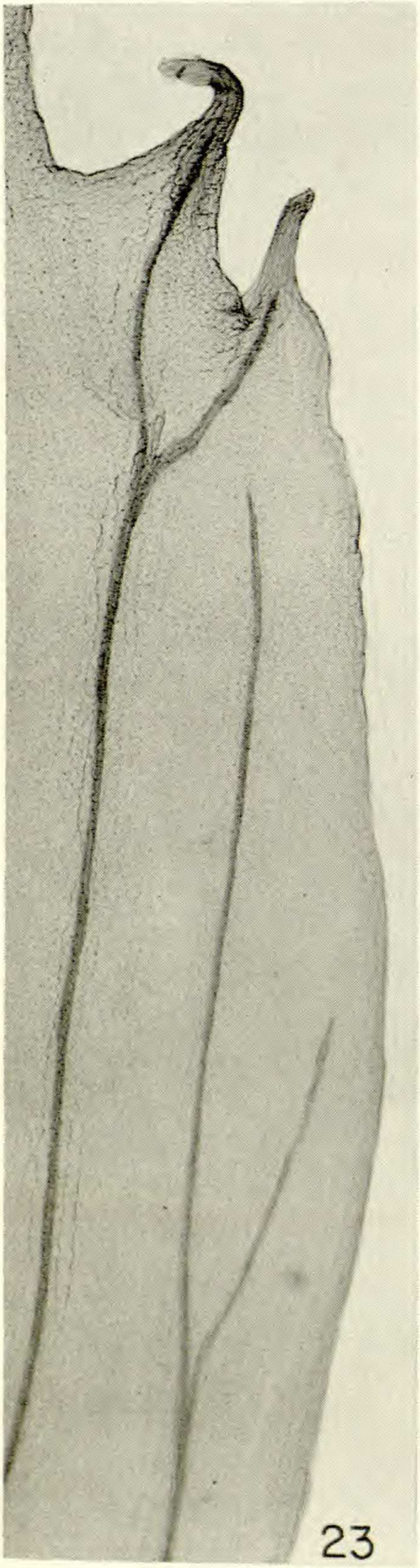
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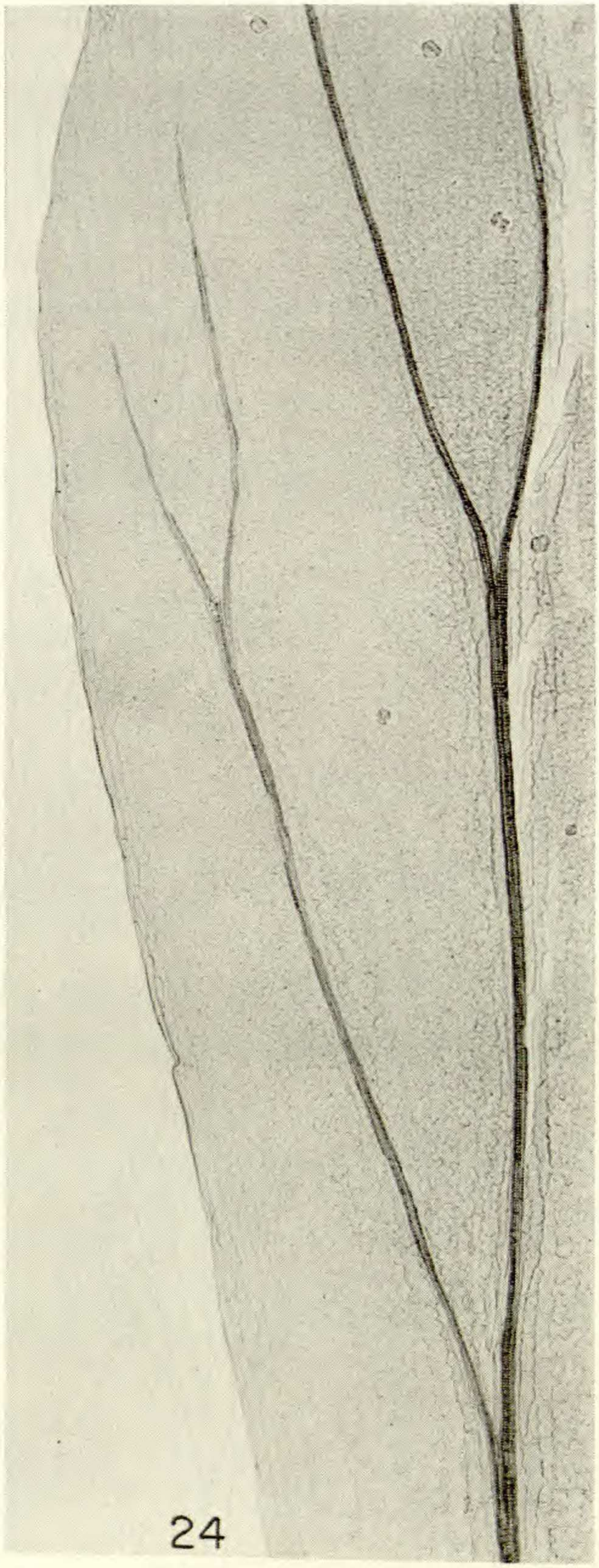
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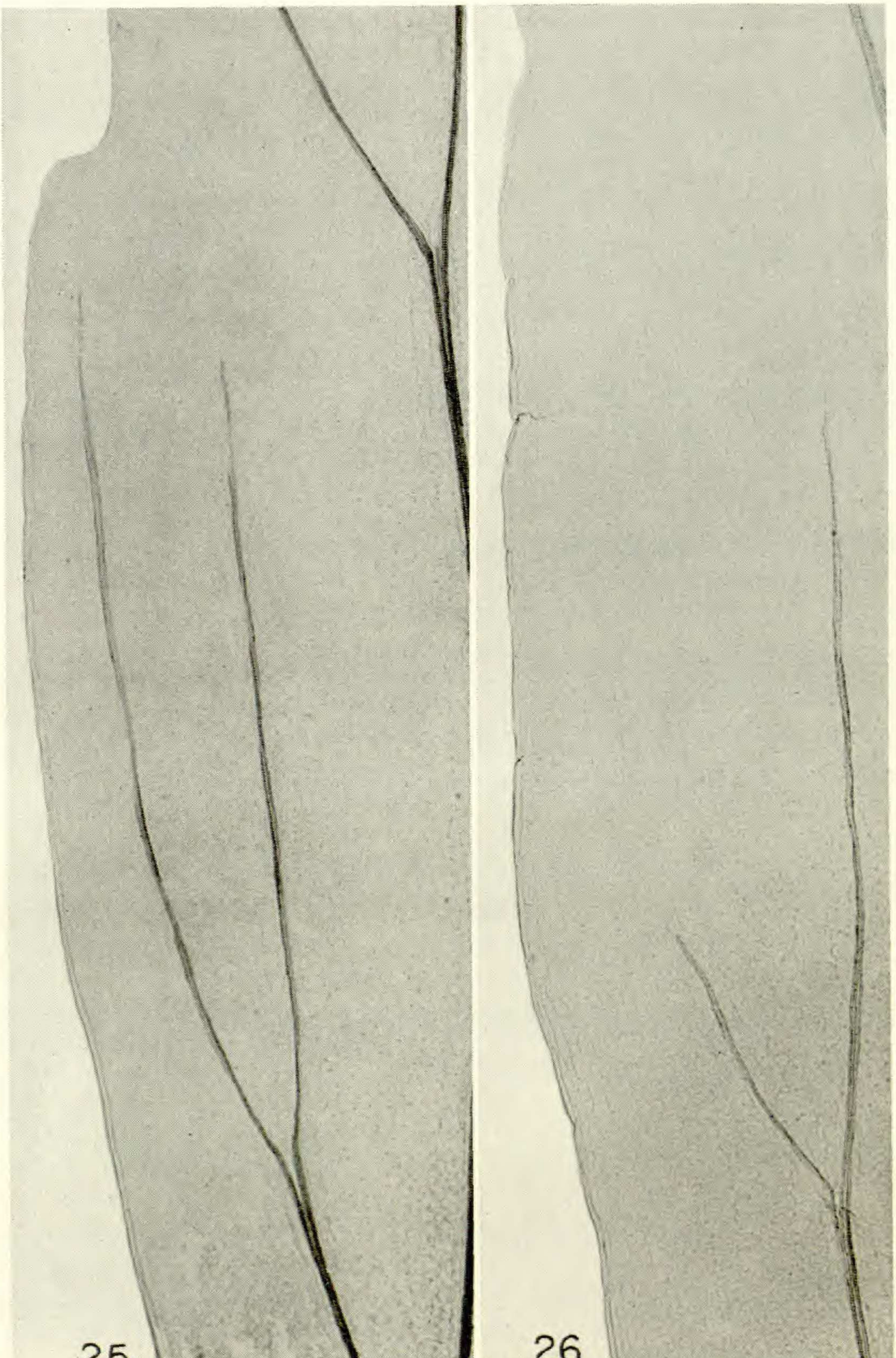

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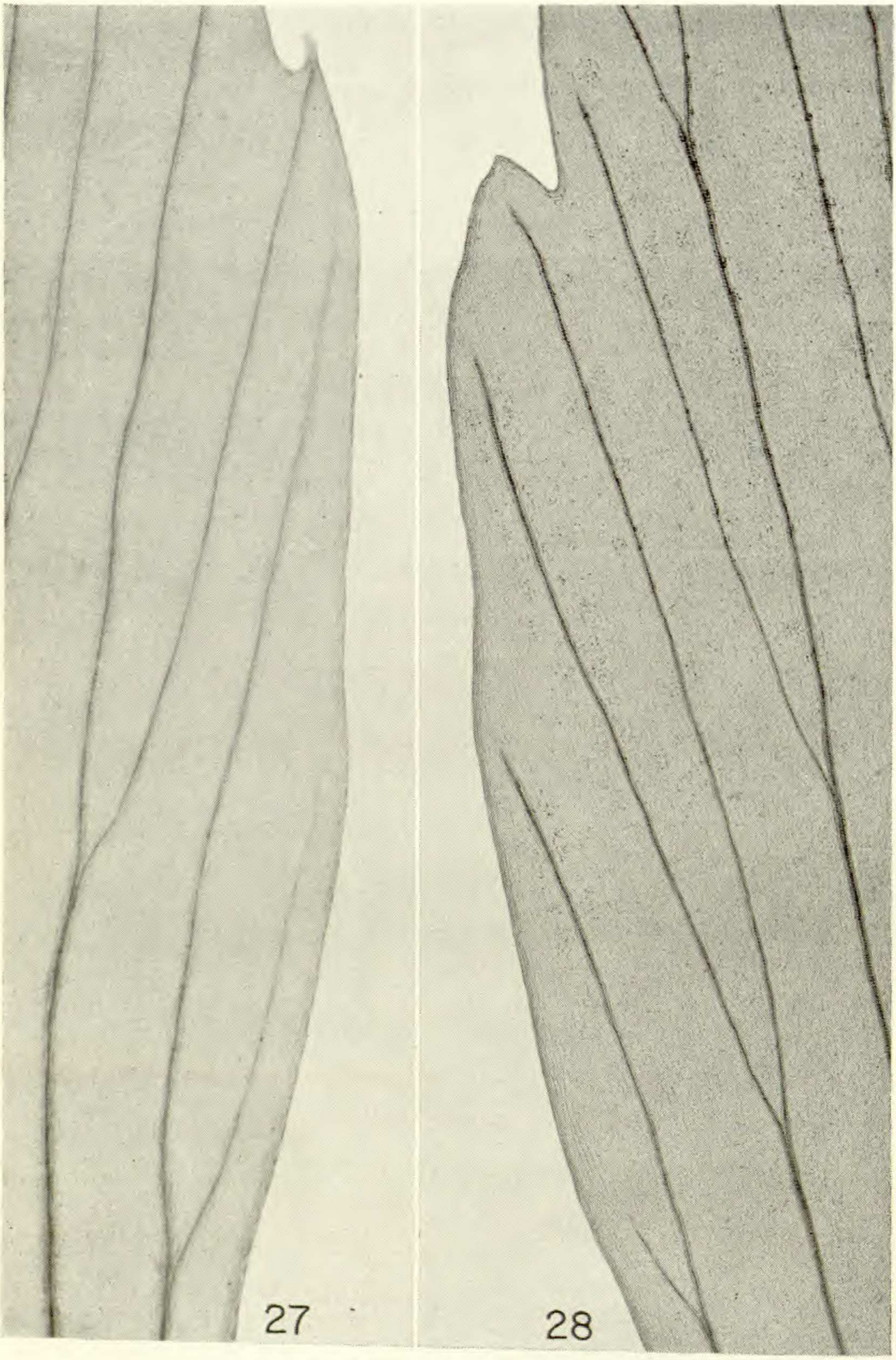

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